RESEARCH PAPER

Soil heterotrophic respiration in *Casuarina equisetifolia* plantation at different stand ages

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Abstract: The soil respiration rates (R_h) in 6-year-old (young), 17-year-old (middle-age), 31-year-old (mature) Casuarina equisetifolia coastal plantations were measured using an LICOR-8100 automated soil CO₂ flux system from May 2006 to April 2007. Results show that R_h displayed an obvious seasonal pattern across the observed years. The maximum values of R_h occurred at June and July and the minimum at December and January. Soil temperature and soil moisture as well as their interaction had significant effects on the monthly dynamics of R_h . The analysis by one-way ANOVA showed that R_h had a significantly exponential relation (p<0.05) to soil temperature at soil depth of 5 cm, and had a linear relation (p<0.05) to soil water content of the upper 20 cm. The result estimated by the two-factor model shows that soil temperature at soil depth of 5 cm and soil moisture at soil depth of 20 cm could explain 68.9%–91.9% of seasonal variations in R_h . The order of R_h rates between different stand ages was middle-age plantation>mature plantation>young-age plantation. With the increase of growth age of plantation, the Q_{10} of R_h increased. The contribution of R_h to total soil surface CO₂ flux was 71.89%, 71.02% and 73.53% for the young, middle-age and mature plantation, respectively. It was estimated that the annual CO₂ fluxes from R_h were 29.07, 38.964 and 30.530 t·ha-1·a-1 for the young, middle-age and mature plantation, respectively.

Keywords: soil heterotrophic respiration; coastal plantation; stand age; Casuarina equisetifolia

Introduction

Soil respiration rates (R_s), or surface soil CO₂ efflux, is the primary pathway of soil carbon release to the atmosphere (Raich & Tufekcioglu 2000). In recent decades, R_s has received more attention because it plays a critical role in global carbon cycle and in global warming feedback (Fang & Wang 2007). The R_s is generally defined as two components, autotrophic respiration (R_a)

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and heterotrophic respiration (R_h) (Kuzyakov & Larionova 2005). In carbon cycle of terrestrial ecosystem, R_h is the main process of soil carbon loss to the atmosphere. Thus, quantifying contribution of R_h to total soil CO_2 effluxes is of great importance and prerequisite for estimating the carbon balance in terrestrial ecosystems (Hanson et al. 2000; Bond-Lamberty et al. 2004).

Most of the previous studies about R_h focus on the inland forest ecosystems (Hanson et al. 2000; Ngao et al. 2007; Saurette et al. 2008; Gaumont-Guay et al. 2008), and very few concerns coastal forest (Tyree et al. 2006). As so far, no available information has been found on R_h in coastal forest ecosystem in China. In coastal regions, forest plantation plays an important role in wind combating, sand fixation and local environment improvement. As the main plantation species, *Casuarinaceae* is widely distributed in southern China, especially in Zhejiang, Fujian, and Guangdong provinces. It was reported that the area of *Casuarina equisetifolia* plantations has been up to 3×10^5 ha in China (Zhong & Zhang 2003).

In this study, the R_h of C. equisetifolia plantation at 3 different growth stages was separated and measured in 2006 and 2007. The main points of the present study were addressed as: (1) seasonal dynamics of R_h ; (2) effects of temperature, soil moisture and forest age on R_h ; (3) contributions of R_h to total soil surface CO_2 flux; and (4) annual fluxes of R_h in the plantations at three different growth stages.



Materials and method

Site description

The experiment site was situated in Chihu State-owned shelter forest of Huian county in Fujian Province, China (latitude 24°30′–24°55′N and longitude 118°40′E–118°55′E,). The study site is at elevation of 5–400 m, with an average slope of <10°. The climate is maritime monsoon climate, with mean annual air temperature of 19.8 °C. The frost-free period is 320 d. Annual

mean precipitation is 1000–1500 mm, with annual mean evaporation of 2000 mm. The typical soil is homogeneity aeolian sand soil with low nutrients, and the layer thickness is 80–100 cm. The forest communities are dominated by *C. equisetifolia* pure plantations with few shrubs and grasses.

Three plantations in different growth stages (6-year-old, P6), (17-year-old, P17), and (31-year-old, P31) were chosen for the study. In each plantation, a plot of 20 m×20 m in size was set up. Before measurement of soil respiration, the characteristics of forest community and soil physiochemical properties were investigated (Table 1).

Table 1. The characteristics of forest community and soil physiochemical properties in C. equisetifolia plantations at three different stand ages

	Community			Soil physiochemical properties (0–20 cm)					
Stand ages	Density (trees·ha ⁻¹)	Average DBH (cm)	Average tree height (m)	pН	Soil bulk density (g·cm ⁻³)	SOC (g·kg ⁻¹)	TN (mg·kg ⁻¹)	C/N	
P6(6-year-old)	2500	5.5	9.5	5.47±0.08	1.22±0.05	7.14±1.14	72.72±3.81	98.21±5.62	
P17(17-year-old)	2202	12.2	10.8	5.24±0.05	1.24±0.05	12.00±1.65	76.90±4.12	156.05±7.73	
P31(31-year-old)	1962	15.1	13.7	5.10±0.05	1.37±0.09	12.43±1.69	81.15±4.26	153.27±7.32	

Measurement methods

In each plantation, the roots were excluded in three subplots (1 m \times 1 m) by using trenching method. Moreover, the total surface soil CO₂ effluxes were measured in one subplot (50 cm \times 50 cm).

 $R_{\rm s}$ and $R_{\rm h}$ were measured at a certain day in the middle of every month from May 2006 to April 2007. Measurements were at hourly intervals throughout a daytime from 08:00 a.m. to 18:00 p.m. Every measurement lasted for 2 min with 3 replicates. In addition, four observations on daily variations (beginning at 08:00 in the morning and ending at 08:00 of next morning) were carried out for each site on July 2006, October 2006, January 2007 and April 2007, respectively.

 $R_{\rm s}$ and $R_{\rm h}$ were measured using an LI-8100 Automated Soil CO₂ Flux System (LiCor Inc., Lincoln, NE, USA) equipped with a short-term chamber. Integrated pump circulates the headspace air from the chamber to the non-dispersive infrared (NDIR) gas analyzer during the closed state of the chamber and the CO₂ concentration data as well as the calculated flux rates are recorded in the system. A PVC soil collar (inner diameter 20.4 cm×7.5 cm tall) was inserted into soil at 5-cm depth on May 2006 in every $R_{\rm s}$ and $R_{\rm h}$ point, and left in the same locations throughout the study period. Meanwhile, all living vegetation aboveground in the plots was removed (don't disturb the litter layer) and the plots were kept free of living plants during the study period.

Simultaneously, air temperature (T_a), surface soil temperature (T_0), soil temperature at a depth of 5 cm (T_5) and soil water content at a depth of 20 cm were measured by a DHM2 ventilated thermometer, convoluted tubule geo-temperature table, the temperature probe belong to the LI-8100 and drying method, respectively.

Data analysis

Daily average flux of R_h according to the daily variations in 24 h \bigcirc Springer

was observed in the four days on July 2006, October 2006, January 2007 and April 2007, respectively. It was found that the effluxes measured during 10:00-12:00 in the morning can basically represent for the daily average flux of $R_{\rm h}$. Kessavalou et al. (1998), Du et al. (2006) and Jin et al. (2007) also used similar treatments in studying the seasonal dynamics of soil greenhouse gases. Therefore, in this study, we used the $R_{\rm h}$ rates during 10:00-12:00 in the morning to represent for the $R_{\rm h}$ daily average flux in the other eight months.

The relationship between R_h and temperature (T) was simulated with an exponential equation and Q_{10} value (defined as the increase in respiration rate per 10°C increase in temperature).

$$R_h = ae^{bT}, Q10 = e^{10b}$$
 (1)

where, a is the basic respiratory (the respiration rate when temperature at 0 °C), b is the temperature sensitive coefficient. The relationship between R_h and soil surface water content (W, volume to volume, 0–20 cm) is simulated with a linear equation.

$$R_h = cW + d (2)$$

where, c and d are the regression coefficients.

Correlation analysis showed that R_h had a better correlation with T_5 than that of T_a and T_0 . So the dependence of T_5 and soil water content (W) on R_h was analyzed by a nonlinear regression model as follows.

$$R_b = a \times e^{bT} \times W^c \tag{3}$$

where, T is the soil temperature at 5-cm soil depth, W is the soil water content, and b and c are regression coefficients.

$$H_{C} = R_{h} / R_{s} \tag{4}$$

where, H_C is the contribution of R_h to total soil surface CO_2 flux.

Calculating of annual CO_2 flux of R_h : firstly, the average daily values of T_a (from an automatic weather station of the forest center) were transformed to T_5 according to their significant correlations and the average monthly values of T_5 were calculated; secondly, combinating with the average monthly value W (3 days per month for each forest type), T_5 was inputted into the nonlinear model (Equation (3)) to get the CO_2 emission of R_h in every month during the study period, and finally, the fluxes in the 12 months were cumulated to get the annual flux of R_h .

We used SPSS 13.0 (SPSS Inc. 2001) to do the statistical analyses. Relationships between $R_{\rm h}$ and $T_{\rm a}$, $T_{\rm 0}$, $T_{\rm 5}$ and W, and the differences among 3 plots were analyzed using the One-way ANOVA. Two-factor regression analyses were made under the nonlinear module. Graphs were prepared by using Excel (Microsoft Corp. 2003).

Results

Seasonal dynamics of R_h

The R_h rate in C. equisetifolia plantation had an obvious seasonal pattern, with a similar single peak curve for each of three growth stages (Fig. 1). In March and April, soil CO_2 efflux stayed at a low level, and increased slowly with the increase of microbial activity resulted by the risen temperature and the improvement of soil water content. It reached the maximum at June (for P17) or July (for P6 and P31) and decreased gradually with the minimum at December (for P6 and P17) or January (for P31). The coefficients of seasonal variation were 23.68%, 36.96% and 30.46% for P6, P17 and P31, respectively.

The mean R_h rate (µmol CO₂ m⁻²s⁻¹, mean±SE) in the three

plots was ranked as: P17 (2.76 \pm 0.085) > P31 (2.17 \pm 0.055) > P6 (2.00 \pm 0.039). Mean multiple comparisons in SPSS, at the 0.05 significant level, showed that there was a significant difference of $R_{\rm h}$ rates between P6 and P17 (p=0.018), but no significant difference was found between P17 and P31 (p=0.060), and between P6 and P31 (p=0.593).

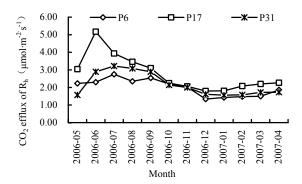


Fig. 1 Seasonal variations of R_h rates for the C. equisetifolia plantations at three different stand ages

Models of R_h to temperature and soil surface water

In this paper, T_a , T_0 , T_5 and W were measured and their effects on R_h were analyzed (Table 2). The influences of temperature on R_h were different among T_a , T_0 and T_5 . The R_h rates had no significant correlations with T_a and T_0 for the three plots except for the relationship between T_a and R_h in the young-age plantation, but had significant relationships with T_5 in all the three growth stages (P<0.05). T_5 could account for 51.73%– 62.87% of R_h variations.

Table 2. Models of R_h to temperature and surface soil water content for the C. equisetifolia plantations at three different stand ages

		$R=ae^{bT}$		R=aW+b		D-	$=a\times e^{bT}\times W^{c}$	
Stand age	T_{a}	T_0	T_5	<i>K</i> −a <i>W</i> +0		K-	-a×e ×w	
	R^2	R^2	R^2	R^2	a	b	c	R^2
P6(6-year-old)	0.5309	0.5908	0.6287	0.5926 (<i>p</i> =0.000)	1.973	0.014	0.114	0.689 (<i>p</i> =0.000)
	(p=0.082)	(p=0.116)	(p=0.000)	0.5720 (p 0.000)				
P17(17-year-old)	0.3239	0.4510	0.5173	0.7865 (p=0.003)	3.731	0.020	0.422	0.919 (<i>p</i> =0.000)
	(p=0.002)	(P=0.067)	(p=0.000)	0.7803 (p=0.003)	5.751			
P31(31-year-old)	0.4750	0.5806	0.6230	0.8207 (<i>p</i> =0.001)	2.262	0.038	0.552	0.901 (<i>p</i> =0.000)
	(p=0.157)	(p=0.719)	(p=0.000)	0.8207 (p-0.001)		0.038	0.332	

Notes: all models were tested at the significance level of 0.05 (two-tailed). T_a , T_0 , T_5 indicate air temperature, surface soil temperature, soil temperature at 5-cm depth, respectively. W means soil water content at 20-cm depth. The temperature indicator in the two-factor model was based on T_5 .

In addition, the Q_{10} values of R_h based T_5 were 1.39, 1.44, and 1.95 for P6, P17 and P31, respectively, which showed that the temperature sensitivity of microbial respiration improved with the increase of stand ages. Kirschbaum (2006) and Fan et al. (2008) summarized the influencing factors of R_h , and pointed out that temperature, moister and the soil substrates were the main factors. In our study, no obvious differences between temperature and soil moister conditions were found among C. equisetifolia plantation at three stand ages; furthermore, soil organic carbon

contents were similar. Soil heterotrophic respiration is the decomposition process of soil organic matter and litter dominated by soil microbial. Hence we hypothesized that the differences of Q_{10} values in our study were mostly likely caused by different temperature sensitivity of litter decomposition in the plantations at different stand ages. Of course, the hypothesis must be tested and confirmed in subsequent study.

The linear models showed that the R_h rate had significant correlation with surface soil water content. Soil water content ac-



counted for 59.26%–82.07% of R_h variations, which stated clearly that the effect extent of soil moisture on microbial respiration was larger than that of temperature because of the sandy soil of coastal protective forest.

The biological processes in R_s can be considerably influenced by soil temperature and moisture, and their interactions correlated to R_s must be considered, so do R_h (Zhang et al. 2005; Wang & Yang 2007), which also was confirmed in our study. Soil temperature at soil depth of 5 cm and moisture at soil depth of 20 cm had better prediction on R_h than using respective independent variable, and R^2 values were 0.689, 0.919 and 0.901 for P6, P17 and P31, respectively.

Contribution of R_h to total surface soil CO_2 efflux and its seasonal pattern

In P6, the $H_{\rm C}$ varied from 65.50% to 78.56%, with an average of 71.89%; while in P31, the $H_{\rm C}$ varied from 66.96% to 81.26%, with the average of 73.53%. In P17, the $H_{\rm C}$ varied from 64.82% to 77.74%, with an average of 71.02% (Fig. 2). However P31 had higher $H_{\rm C}$ than P6 and P17 in most months, and there was no significant difference of $H_{\rm C}$ among the three plantations at different growth ages at 0.05 significant level (P=0.326).

The seasonality of H_C showed a similar pattern for the 3 plots (Fig. 2). From May 2006 to August 2006, the H_C maintained at a low level with an average of 67.51%. H_C increased and peaked on February-March 2007, which showed a reverse seasonality pattern comparing to the air temperature.

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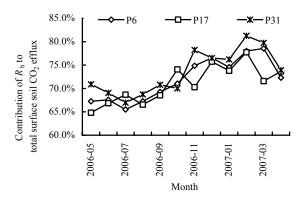


Fig. 2 Seasonal dynamics of the contribution of R_h to total surface soil CO₂ efflux in the *C. equisetifolia* plantations at different growth ages (P6 means 6-year-old; P17, 17-year-old; P31, 31-year-old)

The seasonality of $H_{\rm C}$ showed a similar pattern for the plantations at three different stand ages (Fig. 2). From May 2006 to August 2006, the $H_{\rm C}$ maintained at a low level with an average of 67.51%. $H_{\rm C}$ increased and peaked on February-March 2007,

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which showed a reverse seasonality pattern comparing to the air temperature.

Annual soil CO_2 flux of R_h

The results showed that T_a was significantly correlated to T_5 , and the average of R^2 values in the plantations at three different growth ages reached 0.92 (p<0.05), so the air temperature could be converted to the soil temperature at a soil depth of 5 cm. According to the method mentioned above, we estimated the annual soil CO_2 effluxes of R_h and the values were 29.072, 38.964 and 30.530 t·ha⁻¹·a⁻¹ for the young, middle age and mature plantations, respectively (Table 3).

Table 3. Linear relationships between T_5 and T_a and annual CO₂ flux of R_h of the C. equisetifolia plantations at three different stand ages (t·ha⁻¹·a⁻¹)

Stand age	Linear relationship between	Annual CO ₂		
Statiu age	T_5 and T_a	flux of R_h		
P6(6-year-old)	y = 0.927x + 1.724 ($R^2 = 0.9333, P < 0.05, n = 36$)	29.072		
P17(17-year-old)	y = 0.927x + 1.724 ($R^2 = 0.9333, P < 0.05, n = 36$)	38.964		
P31(31-year-old)	y = 0.895x + 2.851 ($R^2 = 0.8850, P < 0.05, n = 36$)	30.530		

Discussion

 $R_{\rm h}$ and the environmental variables

Our study shows that the mean R_h rate in C. equisetifolia plantations was $2.31\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, which was higher than that of native Castanopsis kawakamii forest (1.88 μ mol CO $_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), monoculture Castanopsis kawakamii plantations (0.82 μ mol CO $_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) and Chinese fir plantations (0.73 μ mol CO $_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) in Fujian Province (Yang et al. 2006). Zhou et al. (2000) reported that the mean R_h rate was 0.94 μ mol CO $_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ in deciduous broad-leaved forest and 1.30 μ molCO $_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ in evergreen broad-leaved forest.

Many reports about soil respiration pointed out that temperature and moisture were the main corresponding environmental factors (Fang & Moncrieff 2001; Rodeghiero & Cescatti 2005). $R_{\rm h}$ is also influenced by both climatic factors and human activity (Jia et al. 2005). Temperature is the main controlling factor of R_h in terrestrial ecosystems and would be regulated by soil moisture (Davidson et al. 2000). When soil moisture was the limiting factor, R_h was not controlled by temperature, and instead, soil moisture became the major driver of R_h . This phenomenon was confirmed by Kucera & Kirkham (1971), Zhou et al. (2004) and Raich & Mora (2005). In this study, air and soil temperatures were maintained at a relatively high level and had little variation, but soil moisture in the coastal sandy soils was very low during the study period (averaged 4.33%). Therefore, surface soil moisture was regarded as the limiting factor of R_h and presented a high relationship with soil heterotrophic respiration. The maximums of R_h appeared on June or July when there were better soil

moisture conditions, compared with soil moisture on August with the highest air temperature.

Contribution of R_h to total soil CO_2 flux

The contributions of $R_{\rm h}$ to total surface soil CO₂ flux varied greatly with different plantations and sampling time. Raich & Tufekcioglu (2000) revealed that $H_{\rm C}$ had a low value in cold biomes, ranging from 7% to 50% in arctic tundra and 11% to 38% in boreal forests. In temperate regions, the $H_{\rm C}$ ranged from 50% to 67% in broad-leaved forests from 38% to 65% in pine forests. Therefore, the trend of increase of $H_{\rm C}$ with temperature increasing in macro-scale is quite clearly. The annual mean air temperature is 19.8°C at this field, so the average $H_{\rm C}$ at 72.15% in the three C. equisetifolia plantations was reasonable.

However trenching method was a mature approach to separate R_a and R_h , which also could affect R_h and its contribution to total surface soil CO_2 flux; for example, Uchida et al. (1998) had pointed that, in the trenched plots, the decomposition of the root residuals could largely enhance the soil heterotrophic respiration and elevate the contribution of soil microbial respiration to total soil CO_2 effluxes. Moreover, temperature and soil moisture would change in the trenched plots, which could also alter the soil microbial activity (Wang & Yang 2007). So far, however, the estimated range of trench effect and how to reduce or even eliminate the trench effect have been not well studied.

In the C. equisetifolia plantations, the H_C varied at different growth seasons. In winter and spring, H_C presented a high value; while in summer and autumn, $H_{\rm C}$ was decreased. The results were agreed with the findings by Zhang XQ et al. (2005) and Chang et al. (2007). Li et al. (2000) reported that soil respiration was mainly contributed by the decomposition of soil organic matter when air temperature was below 15°C; but when air temperature was above 15°C, the contribution of plant root respiration was larger than microbial respiration. In our study, the H_C decreased when air temperature and soil temperature increased. This phenomenon may be attributed to the booming of root metabolic activity and the higher Q_{10} of the root respiration than that of microbial respiration (Boone et al. 1998; Epron et al. 2001). In addition, the higher H_C in winter and spring was partly due to the frequent windy weathers which increased the litter of branches.

Effects of stands at different ages on R_h

Previous studies about the influence factors of R_h in forest communities focused upon soil temperature and moisture (Wang & Yang, 2007; Bauer et al. 2008; Gaumont-Guay et al. 2008; Graf et al. 2008), the extent and mechanism of the effect of stand age on R_s and R_h were not well known. Saurette et al. (2008) reported that there was no significant difference of R_h between plantations at different growth ages. However, the significant difference of R_h was found in this study (p<0.05), the R_h was highest in the middle-age plantation and then followed by the mature plantation. The lowest R_h rate occurred at the young-age plantation. Different growth ages of plantation can influence R_s and R_h by the type

and number of microbial communities (Gao et al. 2007), aboveground biomass (Chapin & Ruess 2001), Quantity and quality of litters (Liu & Fang 1997) and soil quality (Shao et al. 2005). The differences of R_h rates among different forest communities that had similar climatic conditions and soil environment were mainly driven by different quantities and quality of soil respiratory substrates (Ma et al. 2003; Yang et al. 2005). In our study, the C. equisetifolia plantations at three stand ages have the same meteorological conditions and soil physiochemical properties; especially there were no obvious differences of soil organic carbon contents which had low background levels and low contribution of soil mineral respiration to soil heterotrophic respiration. Moreover, the litter quality among the three plantations was similar. Thus, we hypothesize that the differences of R_h rates between the plantations at three growth ages may be attributed to the different litterfall quantity (especially different quantities of fresh litter). This hypothesis need proof in the future study.

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